

COMBRETUM LAXUM JACQ. VAR. EPIPHYTICUM (COMBRETACEAE)

A CASE OF SELECTION FOR WATER DISPERSAL

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Combretum laxum Jacq. is an extremely variable species ranging from Mexico to Argentina and the West Indies. In Mexico and upper Central America it flowers from February to September but mostly in April and May, whereas in South America it flowers July-November, especially during September and October. Fruit morphology in both Central and South America is quite variable, ranging from broadly to narrowly 4-winged. Perhaps due to the influences of the phenologically different races in North America and South America two distinct types of plants have evolved in Panama. The typical plants of Combretum laxum in Panama differ very little from plants of the species in Central and South America. Other plants represented by the name Combretum epiphyticum Pittier are both morphologically and ecologically distinct. Combretum epiphyticum Pittier was described from the Canal Zone but was later included in synonymy by Exell in the Flora of Panama. Although the broad view taken by Exell (1958) is quite appropriate for so complex a species as Combretum laxum, there is also a need for the recognition of the large and consistent differences which occur in Panama. I am therefore proposing to elevate Combretum epiphyticum Pittier to a varietal level of C. laxum Jacq.

Though some of the morphological and phenological features of var. epiphyticum are exhibited in var. laxum elsewhere in Central America, notably the predominantly April-May flowering period and the tendency toward a thicker, narrowly-winged fruit, these features are not correlated in any way except in Panama.

The following key and descriptions are provided to separate the two varieties of Combretum laxum in Panama. An *exsiccatae* is also provided since the two taxa were considered as one in the Flora of Panama treatment.

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Key to varieties of Combretum laxum in Panama

Plants flowering March-April; fruits maturing August-September; young stems, axes of inflorescence and petioles densely ferruginous-tomentose; lower surface of blade conspicuously pubescent; fruit merely 4-angled or if 4-winged, sulcate less than halfway to center of fruit.

var. epiphyticum

Plants flowering mostly October-November (some flowers persisting longer on old inflorescences); fruits maturing January-March; young stems, axes of inflorescence and petioles glabrous or puberulent, never densely ferruginous-tomentose; lower blade surface glabrous or nearly so; fruit prominently winged, sulcate well over halfway to center of fruit.

var. laxum

COMBRETUM LAXUM Jacq. var. EPIPHYTICUM (Pittier) comb. novo  
Combretum epiphyticum Pittier, Contr. U.S. Natl. Herb.  
18: 247. 1917

Shrub or low, sprawling liana usually to 8 m tall. Leaves opposite; petioles 2-7 mm long, densely ferruginous-tomentose; blades ovate-elliptic to oblong-elliptic to obovate, gradually to abruptly acuminate at apex, rounded at base and inconspicuously subcordate (the sinus 2-4 mm deep), 6-16 cm long, 2.5-7 cm wide, lateral veins 10-14 pair, the secondary lateral veins usually continuous between primary laterals, upper surface sparsely short-pilose throughout, somewhat denser on midrib, deciduous in age except along midrib, lower surface similarly pubescent but denser, the trichomes persisting in age. Panicles terminal or upper axillary; branches opposite or in whorls of three, the lower subtended by small leaves, the upper by lanceolate, caducous bracts ca 4 mm long; rachises, peduncles and ovary very densely ferruginous-tomentose; flowers sessile, closely aggregated, subtended by a subulate, caducous bracteole to 1.5 mm long; lower receptacle ovoid, ca 1 mm long; upper receptacle cup-shaped, 1.2-1.5 mm long, including the 4 triangular calyx lobes; petals 4, broadly obovate, white, ca 1 mm diam., glabrous; stamens 8, ca 4 mm long, glabrous; anthers reddish-brown, broader than long, ca .5 mm broad. Fruits ovoid in outline, acute at apex, obtuse at base, 1.7-2.2 cm long, prominently 4-ridged, the ridges sharp, wing-like, the grooves extending less than halfway to center of fruit.

Plants flower in March and April; fruits mature during August and September. The variety is known only from tropical moist forest in the vicinity of the Isthmus of Panama and from tropical wet forest on the Pacific coast in Veraguas Province.

The supposed epiphytic nature of the plant, as suggested by the name and data from the type collection described as "growing on dead tree in lake," is quite uncertain. No subsequent collection has indicated an epiphytic plant. It is quite likely that the species is very tolerant of water and that it may be rooted beneath water, as is true of many other species of trees or lianas.

While light, narrowly-winged fruits tend to be the rule in the genus Combretum, a few such as C. cacoucia Exell and E. laxum var. epiphyticum (Pittier) Croat, have heavier-bodied fruits which are only ridged or with a very narrow wing probably functionless in anemochory. As might be expected, all collections of var. epiphyticum have been made in close association with bodies of water. Fruits are very buoyant and are no doubt largely water-dispersed. Combretum cacoucia also usually grows in association with water and has buoyant fruits. The fact that isolated species of Combretum, belonging to different sections of the genus, have become adapted to hydrochory, strongly indicates that wingless, hydrochorous species have been derived from winged species (Exell, 1958). Since the typical variety is widespread, the implication is that var. epiphyticum has been derived from var. laxum. The alternative of a now extinct ancestor with an unknown fruit type is of course also possible.

CANAL ZONE: Barro Colorado Island; western side of Gross Point Peninsula, Croat 5090 (MO); Coco Solo, U.S. Army Tropic Test Center, Mine Implantation Center, Dwyer & Duke 7879 (MO); Cano Quebrada, growing on dead tree in lake (Gatun Lake), Pittier 6819 (holotype, US), 6668 (US); Gatun in swamps, Hayes 7 (MO); Summit Garden, cultivated? C. Callen 376 (MO).

VERAGUAS: Bahía Honda, near Pueblo Nuevo, Barclay 2831 (MO) (This collection was made in 1839).

COMBRETUM LAXUM Jacq. var. LAXUM, Enum. Pl. Carib. 19. 1760

For a complete synonymy see Exell (1958), Flora of Panama

Liana. Leaves opposite or subopposite,  $\pm$  glabrous; petioles 2-7 mm long; blades lanceolate to oblong-elliptic or ovate-elliptic, acuminate at apex, obtuse to rounded and

inconspicuously subcordate at base (sinus 1-2 mm deep), 10-17 cm long, 3-6 cm wide, subcoriaceous, prominently arched along midrib, drying dark, glabrous to inconspicuously puberulous on lower surface and often pubescent in axils of lower surface, often inconspicuously punctate below. Panicles terminal or upper axillary; flowers sessile, white or yellowish, very fragrant, 4-parted; lower receptacle ovate-oblong, densely dark-strigose in lower 2/3, sparsely so above and on upper receptacle, the latter cup-shaped, ca 1.5 mm long including lobes; calyx lobes broadly triangular; petals rounded, ca 1 mm wide, white, spreading, ± clawed at base; stamens 9, ca 4 mm long, exserted; style to 4 mm long. Fruit ovoid to sub-orbicular, emarginate at apex, cordate at base, 1.5-2 cm long, 1.5-1.7 cm wide, yellowish-brown, 4-winged, the wings to 7 mm wide, the body of fruit to 4 mm wide.

Flowers mostly October and November but with flowers persisting sometimes until February. Fruits mature January to March. Ranges from Mexico to Northern Argentina.

The type of Combretum laxum is from Santo Domingo. West Indian material of the species is close to that of upper Central America. Leaf blades are usually glabrous, except for axillary tufts. They are not at all or only moderately punctate. Plants in Panama and South America are usually glabrous or sometimes only with inconspicuous axillary tufts. Most South American specimens are conspicuously punctate and also often have lepidote scales.

CANAL ZONE: Barro Colorado Island: Aviles 18 (F, MO); Shoreline south of Colorado Point, Croat 7883 (MO); Cove south southeast of Pena Blanca Pt., Croat 8405 (MO); First cove south of Barbour Point, Foster 1327 (DUKE, F, MO, PMA); East shore of Pena Blanca, Foster 1412 (DUKE, MO, PMA); Pearson Inlet, Shattuck 685 (F, MO); Drowned forests along Rio Chagres between junction with Rio Pequeni and Rio Indio, alt. 66 m, Steyermark & Allen 16774 (MO).

DARIEN: Rio Sabana, 0-4 mi from Santa Fe, Duke 4125 (MO); Rio Tuira, between R. Penusa and R. Mangle, Duke 14631 (MO).

PANAMA: Vicinity of El Llano, Duke 5804 (MO); Woods along Pan-Am Highway ca half way between El Llano and Rio Mamoni, Duke 5608A (MO); Drowned forests of Quebrada Tranquilla and its branches, 70-80 m., Dodge & Allen 17501 (MO).